THE INFLUENCE OF THE UTRICLE AND THE EFFERENT VESTIBULAR ACTIVITY ON THE SPONTANEOUS AFFERENT ACTIVITY OF THE NERVES OF THE HORIZONTAL CANAL AND THE ANTERIOR VERTICAL CANAL IN THE FROG

J. Caston

Translation of: "Influence de l'utricule et de l'activite vestibulaire efferente sur l'activite afferente spontanee des nerfs du canal horizontal et du canal vertical anterieur chez la grenouille," "Journal de Physiologie," Volume 62, Paris, 1970, pp. 407-420.

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16. Abstract

Spontaneous activity was studied in the horizontal and anterior semicirculat canal nerves of the frog. Recordings were made with isolated heads (section being performed behind the medulla oblongata), in one group with the intact preparation, after section of the utricular nerve, and on the peripheral end of the cut ampullar nerve; in a second group with the intact preparation, after destruction of the encephalon, and with the peripheral end of the cut ampullar nerve. It was found that spontaneous activity decreases in most cases after section of the utricular nerve; decreases, increases, or remains the same after destruction of the encephalon; at the peripheral end of the cut nerve it always at least equals but mostly is greater than that recorded with the intact preparation and after the two previous tests. The ampullae of the horizontal and anterior canals are innervated by efferent fibers (some related to the utricle) and by collaterals from fibers of the utricular nerve. The former are inhibitory, the latter facilitatory; afferent spontaneous activity is always modulated by these two antagonistic influences.

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THE INFLUENCE OF THE UTRICLE AND THE EFFERENT VESTIBULAR ACTIVITY ON THE SPONTANEOUS AFFERENT ACTIVITY OF THE NERVES OF THE HORIZONTAL CANAL AND THE ANTERIOR VERTICAL CANAL IN THE FROG

J. Caston[1]

Earlier studies (Caston, 1968) have shown that frogs that are only blind[2] /407* and frogs blind and deprived of the two utricles displayed different behavior upon rotation in a horizontal plane: the rotation reactions are fainter in the frog both blind and deprived of the two utricles than in an animal that is only blind. It can thus be assumed that the utricle modifies the activity of the ampulla of the horizontal canal. Before determining by electrophysiological methods if the destruction of the utricle modifies this activity when the ampulla is stimulated, we wished to know whether or not the spontaneous activity that is observed in the nerve of the horizontal canal is modified by the absence of the utricle. In order to interpret the results obtained, we decided in one case to cut the nerve in the horizontal canal of these same frogs, and record the activity at its periphery, and in another case, with other frogs, to compare the activity of the nerve in the horizontal canal before and after destruction of the encephalon. Finally, wholly identical experiments performed in the nerve of the anterior vertical canal have allowed us to learn whether the two ampullae, that of the horizontal canal and that of the anterior canal, are influenced by the same factors.

Techniques /408

The recordings were made with the isolated head of the green frog *(Rana esculenta L.)*, section of the head being done behind the medulla oblongata. The opening of the labyrinthine capsule reveals the anterior horizontal and vertical semicircular canals as the utricle. An electrode of silver chloride,

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[2]Vision modifies rotation reactions, and in order to study the reactions which are of a purely vestibular origin, suppression of visual stimulation is needed.

*Numbers in the margin indicate pagination in the foreign text.

refined electrolytically and having a hooked end, is passed under one of the ampullar nerves by means of a De Fonbrune micromanipulator. The nerve is then carefully lifted in such a way that the part in contact with the electrode does not touch the perilymph. A drop of paraffin oil is placed in the labyrinthine cavity so as to protect the nerves and receptors from desiccation. The neutral electrode, also of silver chloride, is inserted either in a muscle, or, most frequently, under the skin. The preparation is grounded. The electrodes are connected to the input of an oscilloscope by means of a differential preamplifier. Photos were taken image by image. A total of 186 frogs were studied; in each of them spontaneous activity was recorded either in the nerve of the horizontal canal or in the nerve of the anterior vertical canal before and then after the labyrinthine or encephalic lesions indicated in the introduction had been made. The results that we are going to report are somewhat crude and subjective because the recordings were made in the whole nerve. It appears impossible, in fact, to quantify the results rigorously, and this study must only be considered as an approach to the problem we are attempting to resolve. The tracings that have been recorded show significant variations in spontaneous activity after the different operations effected. Nevertheless, only a more precise study, one involving the use of microelectrodes, could give a more objective value to the results.

Results.

I. Semicircular Canals and Utricle.

A). Activity Recorded on the Nerve of the Horizontal Canal.

Spontaneous activity has been identified as such for several reasons; it disappears completely when a drop of ether is placed in the labyrinthine cavity or when a crystal of procaine is placed on the ampulla of the canal studied. It also disappears after puncturing of the ampulla; it increases on rotary stimulation which provokes, in the horizontal canal studied, an ampullopetal flow of endolymph and decreases or ceases upon inverse rotation, which causes, in this same canal, an ampullofugal liquid flow.

1. Spontaneous Activity Before Section of the Utricular Nerve.

Spontaneous activity is present in all cases and persists for several hours. This has already been shown by several authors, particularly by Ledoux (1958). It varies from one frog to another in frequency and in amplitude. The mean amplitude of the spikes is from 10 to 15 μv.

2. Spontaneous Activity After Section of the Utricular Nerve. /409

If the profiles are compared before and after operation for every frog studied, it may be stated that with the exception of two frogs (out of 60), in which spontaneous activity is greater after the test, the activity diminishes or remains unchanged after the suppression of the utricles: diminished in 3/4 of the frogs, and unchanged in 1/4. For the same frog, it seems that the change in amplitude of the spikes is, in general, in the same direction as the change in their frequency (Figure 1). We can only hypothesize to explain this phenomenon that the increase in amplitude that generally accompanies an increase in frequency may be due to a summation of unit potentials, a summation that would be the more substantial as the frequency of the discharges would be greater, or it may be due to excitation of the fibers, until then dormant, fibers whose discharges would be of considerable amplitude.

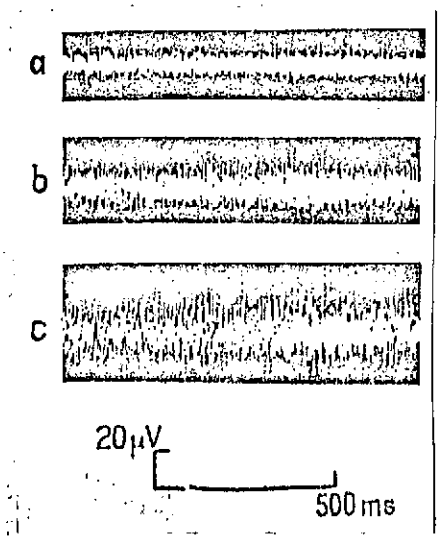

Figure 1. Spontaneous Activity Recorded in the Nerve of the Horizontal Canal. a, Before section of utricular nerve; b, after section of utricular nerve; c, at peripheral end of cut nerve.

3. Spontaneous Activity at the Peripheral End of the Nerve of the Horizontal Canal.

In 19 frogs among the 60 preceding, the nerve of the horizontal canal was cut and the activity at the peripheral end of the nerve was recorded. In most frogs (18 out of 19), a considerably higher activity is seen compared to that which is seen in the intact nerve before section of the utricular nerve: the amplitude of the spikes is currently 20 μv, 30 μv, and may even reach 50 μv.

These recording conditions favor spontaneous activity for purely electrical reasons, the peripheral end being raised and attached to the electrode. Although all the necessary precautions were taken to eliminate this element in recording, we wanted to show that the increase in activity observed is based on physiological phenomena and is not artificial. To do this, with the electrode slipped under the intact nerve in the manner described in the section on /410
"Techniques", we coagulated the nerve for a very short distance between the electrodes and the centers with a very weak current. This coagulation, that amounts, in fact, to isolating the nerve and its receptor at the same time from the centers and other vestibular organs (analogous conditions to those of recording at the peripheral end of the severed nerve) causes a very important increase in spontaneous activity. Furthermore, section of the nerve between the electrode and the coagulated zone does not alter the preceding activity; this last is increased to the same extent in relation to the activity recorded in the intact nerve. Thus, when the nerve is cut and the activity on the peripheral end recorded, the increase in this activity is indeed due to isolation of the ampulla from the centers and other receptors and not to an electrical artefact.

4. Comparison of all the Preceding Results.

a). Two Frogs:

The activity recorded at the peripheral end of the severed nerve is greater than that recorded in the intact nerve before section of the utricular nerve; it is also greater than after elimination of the utricle. Finally, as has already been indicated (I, A, 2), spontaneous activity in the intact nerve was greater after section of the utricular nerve than before (Figure 1).

b). Eleven Frogs:

The activity recorded at the peripheral end of the severed nerve is always higher than that recorded on the intact nerve after section of the utricular nerve (Figure 2A, 2B, 2C); it is usually higher (Figure 2A) or equal (Figure 2B) to that recorded before section of the utricular nerve (it is lower in only one case: Figure 2C). In the case of 11 frogs, section of the utricular nerve caused a more or less significant decrease in activity in the ampullar nerve.

c). Six Frogs:

The discharges observed at the peripheral end of the severed nerve are higher than those recorded in the intact nerve, before as well as after elimination of the utricle; section of the utricular nerve does not greatly modify the activity recorded in the ampullar nerve (Figure 3).

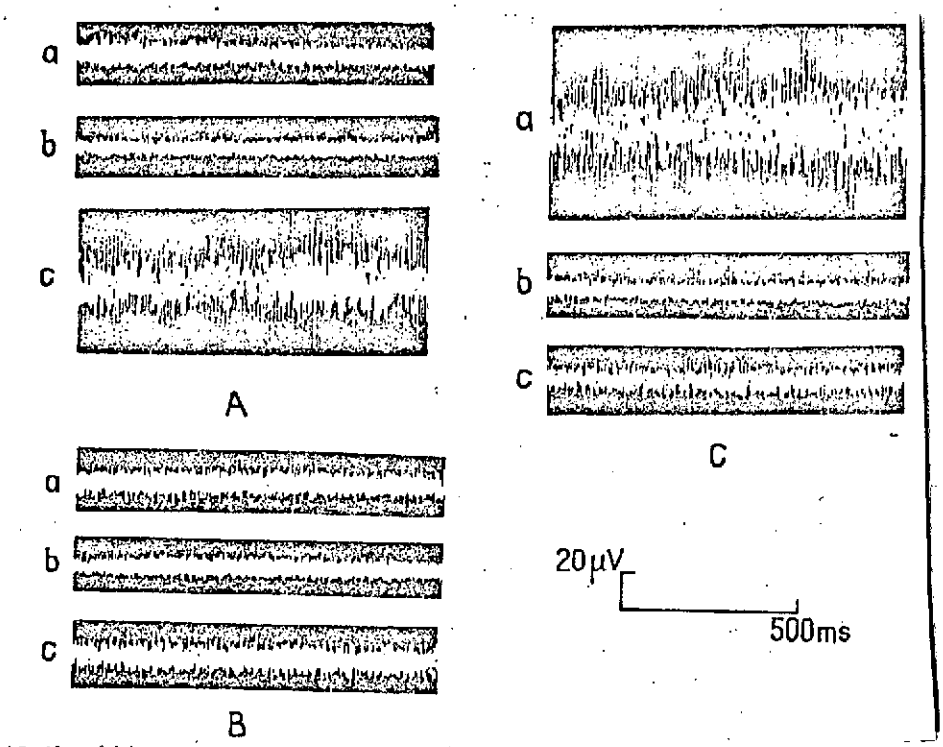

Figure 2. Same Caption as Figure 1. Tracings A, B and C were recorded on three different preparations.

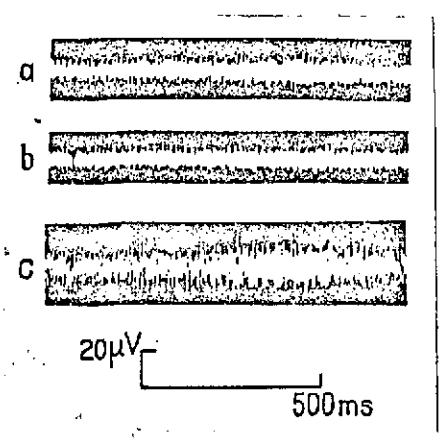

Figure 3. Same Captions as Those for Figure 1.

B). Spontaneous Activity Recorded in the Nerve of the Anterior Vertical Canal.

The same experiments were performed in the nerve of the anterior vertical canal on 33 frogs; similar results were found. In fact, study of the profiles shows that in a minority of frogs (3) section of the utricular nerve involves a recrudescence of activity in the nerve of the anterior canal. Among most frogs (22) this same intervention involves a more or less significant decrease in discharges /411

(which may even be eliminated), whereas among the remaining frogs (8), elimination of the utricle has no effect. Comparison of the activity recorded in the nerve of the anterior canal before and after section of the utricular nerve, and at the peripheral end of the ampullar nerve done on 17 frogs, yields /412 results very similar to those obtained in the nerve of the horizontal canal.

C). Findings From Experiments on the Two Ampullar Nerves.

The following conclusions may be drawn from the totality of the results obtained in these two ampullar nerves:

1. The activity recorded after section of the utricular nerve is greater, equal to, or lower than that recorded before the operation: it is most often lower (in 70% of 93 preparations); it is equal much less often (in 25%); and is higher in only five cases (5%).

2. The activity recorded at the peripheral end of the severed nerve is, with one exception, at least equal and most often greater than the activity recorded in the intact nerve before section of the utricular nerve.

3. The activity recorded at the peripheral end of the severed nerve is greater or at least equal to that recorded in the intact nerve after section of the utricular nerve, even when this operation has the effect of increasing activity. In other words, the activity recorded at the peripheral end of the nerve is always higher or at least equal to all other kinds of activity. Thus, the elimination of the utricle causes in the anterior horizontal and vertical ampullar nerves a decrease in spontaneous activity, the latter being eliminated in the end. These results are in complete accord with those obtained in a study of the frog on a rotary platform (Caston, 1968); after section of the utricular nerves, the rotatory reactions in the case of one-fourth of the frogs were identical or very slightly weakened in relation to those observed before section; three-fourths showed greatly weakened reactions (some of them even showed no more movement). It can thus be said that the presence of the utricle facilitates the activity of the ampullar receptor studied (a more or less substantial facilitation, eliminated at the limit). Thus a relationship exists between the utricle and the ampullar receptors. This relationship could be effected through the intermediary of centrifugal fibers innervating the ampullae

of the canals studied, ones whose activity would depend on the utricle. This theory is based on the one hand on the studies by Schmidt (1963), Gleisner and Henriksson (1963), and our own (Caston, 1970b), which shows that stimulation of the horizontal canal by rotary acceleration causes the appearance of discharges at the level of other branches of the vestibular nerve detached from their receptors, and on the other hand, on results obtained showing the existence of an efferent spontaneous vestibular activity (Schmidt, 1963; Caston, 1970a). These relationships could also be established by collaterals coming from utricular fibers, collaterals terminating in the ampullae studied. To decide between these two theories, we were led to examine the influence of the centrifugal system on the activity of the nerve of the horizontal canal and on the nerve of the anterior vertical canal. To do this, a second series of experiments were performed in which the activity of the fibers of the ampullar nerves before and after destruction of the encephalon were compared with that recorded at the peripheral end of the severed nerve. /413

II. Semicircular and Encephalic Canals

A). Spontaneous Activity Recorded on the Horizontal Canal Nerve.

1. Comparison Between Spontaneous Activity Recorded on the Intact Nerve Before and After Destruction of the Encephalon.

Of 62 animals studied it is to be noted that in slightly more than half of the cases the activity observed before and after destruction of the encephalon is the same: in one-fourth of the cases it diminishes considerably and may even vanish; finally, of the remaining animals, destruction of the encephalon is followed by an increase in spontaneous activity.

2. Comparison Between Spontaneous Activity Recorded on the Intact Nerve and at the Peripheral End of the Horizontal Canal Nerve.

The tracing studies with 31 frogs provide the following results:

- encephalon intact:

Among 9 frogs there is no difference between the spontaneous activity recorded at the peripheral end of the nerve, on the one hand, and on the intact nerve on the other; of the other animals in this group (22 frogs), the activity detected is higher at the peripheral end of the nerve than in the intact nerve.

- encephalon destroyed: /414

In the case of 5 frogs, no difference between the activity recorded was observed on the one hand at the peripheral end of the severed nerve, and on the other hand in the intact nerve; in the case of 26 frogs, the activity at the peripheral end is the most important. For each frog, the activity recorded may be compared in the horizontal ampullar nerve before destruction of the encephalon, after this destruction, and at the peripheral end of the nerve.

a). In 3 animals, after destruction of the encephalon the spontaneous activity recorded on the ampullar intact nerve is increased (Figure 4A and B); at the peripheral end of the nerve it is higher (Figure 4B) or at least equal (Figure 4A) to this last.

b). Of 10 frogs, the activity in the nerve of the horizontal canal /415 diminishes after destruction of the encephalon (Figure 5A and B); at the peripheral end of the nerve the spontaneous activity is greater (Figure 5B) or at least equal (Figure 5A) to that recorded on the nerve before destruction of the encephalon.

c). Finally, in the remaining 18 frogs, no difference is noted between the activity recorded before and after destruction of the encephalon (Figure 6A and B); at the peripheral end of the ampullar nerve it is equal (Figure 6A) or greater (Figure 6B) than the preceding; it is never lower.

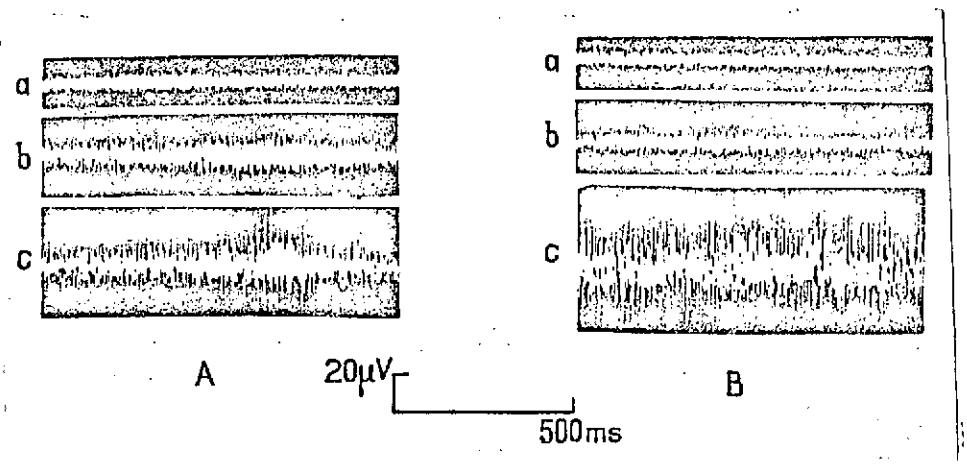

Figure 4. Spontaneous Activity Recorded on Nerve of Horizontal Canal. a, Before destruction of encephalon; b, after destruction of encephalon; c, at peripheral end of severed nerve. Tracings A and B were recorded on two different preparations.

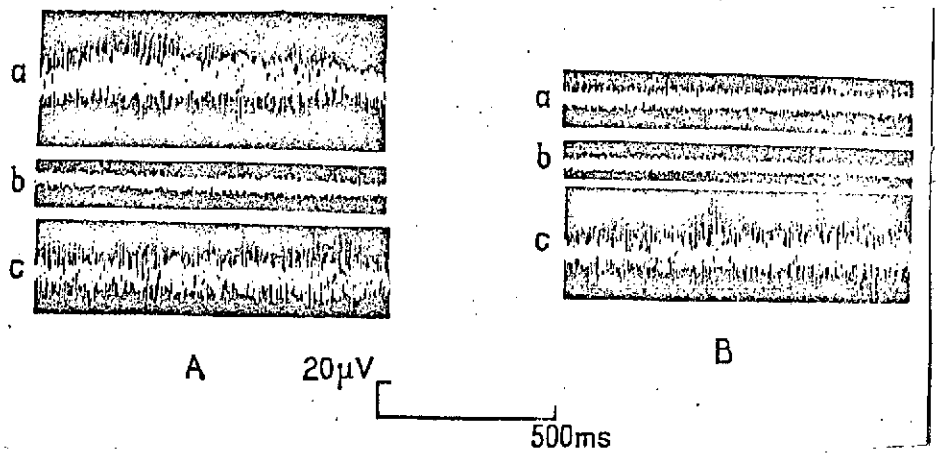

Figure 5. Same Caption as for Figure 4.

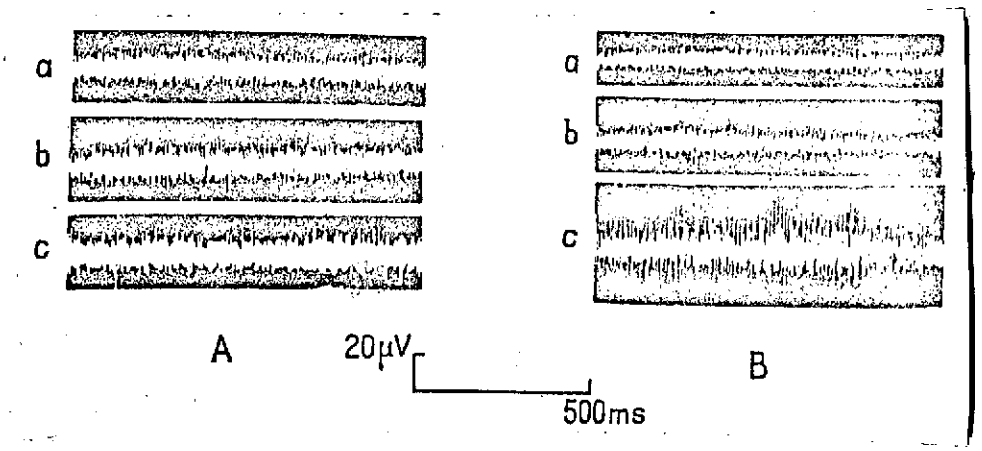

Figure 6. Same Caption as for Figure 4.

B). Spontaneous Activity Recorded on the Anterior Vertical Canal Nerve.

In the nerve of the anterior vertical canal, the results obtained on 31 frogs are similar to those above. After destruction of the encephalon, the activity recorded in the nerve of the anterior canal increases in 7, diminishes in 13, and no difference is observed in the remaining 11. Comparison of the activity recorded before destruction of the encephalon, after this destruction, and at the peripheral end of the nerve yields results identical to those obtained in the nerve of the horizontal canal.

C). Findings

From all the results obtained on the two ampullar nerves it may be concluded that the encephalon does or does not have an effect on their activity; when the encephalon is involved, this effect is either facilitating or inhibiting. Moreover, it can be seen here again that the activity observed at the peripheral end of the nerve is higher or at least equal to that of the intact nerve, whether the encephalon is present or not. Finally, it must be noted that in the case of some 30 frogs, the spontaneous activity of the nerve of the horizontal canal and that of the nerve of the anterior canal was recorded on the same preparation, before and then after destruction of the encephalon. In half of the cases, the activity of the horizontal canal behaves in the same manner as that of the anterior vertical canal; when, after destruction of the encephalon, the activity increases in the nerve of the horizontal canal, it increases equally in the nerve of the anterior canal; when it diminishes in one, it diminishes also in the other; when the destruction of the encephalon does not involve any change in spontaneous activity, it is in both the nerve of the horizontal canal and in the nerve of the anterior vertical canal. A few differences are seen in the other half of the cases: in effect, after destruction of the encephalon, when the activity is modified in one direction or another in the horizontal ampullar nerve, it is not in the nerve of the anterior canal; conversely, when the spontaneous activity is not modified in the nerve of the horizontal canal, it may be either increased or weakened in the nerve of the anterior canal. It is, however, significant to note that in any case an increase in spontaneous activity in one of the two ampullar nerves is not accompanied by a decrease in the activity in the other. It can also be confirmed that the variations provoked in the activity of the two ampullar nerves by the destruction of the encephalon are never in the opposite direction.

Discussion. /416

To say that the discharges at the peripheral end of the severed nerve are greater than in the intact nerve — whether the utricle or encephalon are destroyed or not — amounts to saying that the whole encephalon and utricle exert an inhibiting effect on the afferent activity. Various authors have

shown that excitation of encephalic regions assumed to be related to the vestibular efferent system causes a decrease in the response of the ampullar nerves to a stimulus (Rossi, 1964; Sala, 1965). Besides, efferent discharges have been obtained in vestibular nerves detached from their receptors by stimulation of a single receptor (Schmidt, 1963; Caston, 1970b). The activity of the efferent system would depend on the afferent discharges and would be inhibitory. Thus, the afferent activity of utricular origin would be capable of increasing the efferent activity, and the latter of inhibiting the functioning of other receptors. Electron microscope studies (Wersall, 1956) and results obtained by the techniques of histochemistry (Ireland and Farkashidy, 1961) suggest that efferent vestibular fibers terminate at the receptors. Section of the utricular nerve in diminishing the activity of the efferent pathways should thus produce an increase in the activity of other receptors and particularly of the ampullae studied. The fact that elimination of the utricle in the majority of the cases causes an inhibition of the spontaneous ampullar activity suggests that the lesion made should provoke either the elimination of an excitatory influence or the reinforcement of an inhibitory cause which may be greater than the facilitation due to the suppression of efferent influx. The first supposition is plausible; in fact, if collaterals from utricular fibers exist, ones which innervate the ampullae, these collaterals will similarly have the same function as the afferent fibers from which they came: they will thus be excitatory; section of the utricular nerve would thus eliminate this excitatory influence. As for the second supposition, it would not seem plausible to us; in fact, inhibitory influences other than efferent innervation cannot be envisaged and it does not seem possible that the suppression of certain afferent influences (in this instance, those which come from the utricle) may increase the efferent activity. We propose, therefore, the hypothesis that a balance exists between the facilitating effects of the collaterals of utricular fibers and the inhibitory effects of the efferent fibers. The first would be the most important in 70% of the cases (when section of the nerve of the utricle causes a reduction in discharges); at times no spontaneous efferent activity exists (Schmidt, 1963; Caston, 1970a); only the collaterals would thus play a role, and section of the utricular nerve would hence cause a very important decrease in the ampullar discharge, the absence of facilitation not being compensated by

a rise in inhibition; this fact could even explain the total suppression of ampullar activity which is sometimes observed. These two effects are approximately compensated when elimination of the utricle does not modify the activity of the ampullar nerves. In contrast, if the inhibitory effect of the efferent /417
system dominates, suppression of the utricle would cause an increase in discharges in the ampullar nerves: this case is only found among a few frogs.

This theory explains at the same time the apparently contradictory results obtained in frogs with the encephalon destroyed. Destruction of the encephalon eliminates the inhibitory action of the vestibular efferent system; the afferent activity of all the receptors are thus found to be increased, and the ampullar activity in particular. Moreover, collaterals from fibers where the activity is greatest and whose action would be facilitory would cause a still more substantial increase in the spontaneous activity: this is what is found among certain frogs. The absence of modification of spontaneous activity after destruction of the encephalon can be explained by an absence of spontaneous efferent activity. These results were observed in 45 out of 93 frogs (48%). With regard to this it is interesting to note that in earlier experiments no spontaneous efferent activity was recorded in 23 out of 43 frogs or in almost half of the cases (Caston, 1970a). The decrease in spontaneous activity that is observed after destruction of the encephalon in one-third of the cases can be explained thus: spontaneous efferent potentials may be recorded on the ampullar intact nerve, and the activity collected thus represents the sum of the afferent and efferent factors. The destruction of the encephalon involves both an increase of inhibition and a disappearance of the efferent potentials which are no longer recorded. If the latter was of great frequency, it could be that their disappearance masks a rise in inhibition to a point at which a decrease of overall activity on the intact nerve can be observed.

All these results are thus explained by modulation of spontaneous activity by facilitory and inhibitory influences. This equilibrium is upset in either one direction or another according to the magnitude of these reciprocal influences when the functional state of the vestibular apparatus is modified. At the peripheral end of the cut nerve, the frequency and the amplitude of the afferent discharge being, in the majority of cases, greatly amplified, suggests

that in the case of the intact animal, the aggregate of inhibitions plays a more important role than the aggregate of facilitations. Nonetheless, after destruction of the encephalon, the inhibition is eliminated and the afferent activity of the receptors is no longer modulated, again according to our hypothesis, except through facilitory influences coming from the collaterals of fibers issuing from other vestibular receptors. The pure afferent activity recorded at the peripheral end of the cut nerve, no longer being subject to these facilitations, should therefore be lower than that recorded on the intact nerve with the encephalon destroyed. The increase in activity is due to the increase in inhibitory influences which are at the present time unknown to us. Nevertheless, we can state that these inhibitory influxes are of peripheral origin. In fact, a certain amount of activity is recorded in the nerve of the horizontal intact canal, and this on a preparation where the encephalon is destroyed and where the nerves of all the vestibular receptors, except that of the horizontal canal, have been cut. When the nerve of the horizontal canal is cut and activity at the peripheral end is recorded, it can be stated that the /418 latter is always higher than the preceding. These results, based only on a dozen frogs, suggest the existence of a retroactive inhibitory circuit of the receptor on itself.

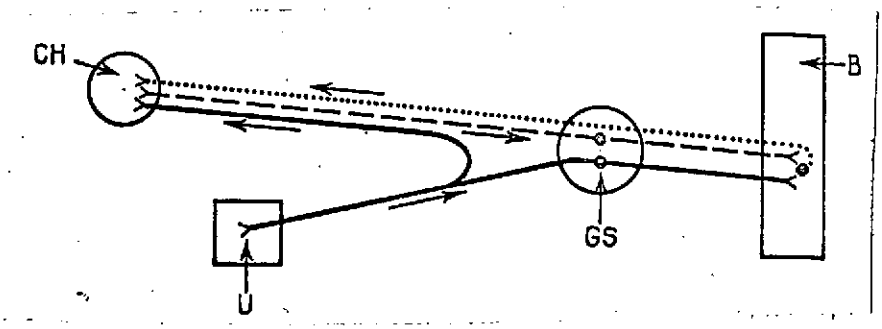

Figure 7. Diagram Showing Relationships Between Horizontal Canal and Utricle. B, Medulla oblongata; C.H., horizontal canal; G.S., ganglion of scarpa; U, utricle. Solid line, afferent utricular and collateral fiber; broken line, afferent ampullar fiber; dotted line, efferent fiber. The arrows along the fiber tracks represent the direction of the influx.

The interpretations that we have given may, insofar as the horizontal canal is concerned, be represented diagrammatically with respect to the relationships between the utricle and this canal (Figure 7). This drawing would be identical for the anterior vertical canal. It should be noted, however, that this drawing does not absolutely rule out central connections; the organization of the vestibular nuclei are not known in the frog, and in particular, the relationships between the efferent neurons and the afferent fibers coming from different vestibular receptors are unknown.

Summary.

Spontaneous activity has been studied on the nerves of the horizontal and anterior semicircular canals of the frog. Recordings have been made with isolated heads (section of the head being performed behind the medulla oblongata):

- in the first group of animals, firstly with the preparation intact, then after section of the utricular nerve, and lastly on the peripheral end of the cut ampullar nerve;

- in a second group, first with the preparation intact, then after destruction of the encephalon, and lastly with the peripheral end of the cut ampullar nerve.

Study of the recordings shows:

1. that the spontaneous activity in most cases decreases after section of the utricular nerve;

2. that the spontaneous activity decreases or increases, or remains the same after destruction of the encephalon;

3. that the spontaneous activity recorded on the peripheral end of the cut nerve is at least always equal, and in most cases greater than that recorded with the preparation intact and then that recorded after the two previous tests.

The interpretation of these results is as follows: the ampullae of the horizontal and anterior canals are innervated by efferent fibers (some of which are also associated with the utricle) and by collaterals from fibers of the

utricular nerve. The first ones would be inhibitory, the second ones facilitory; the afferent spontaneous activity is always modulated by these two antagonistic influences.

REFERENCES

1. Caston, J., "Influence of Elimination of Utricles on Reactions Due to Stimulation of the Horizontal Semicircular Canals in the Frog," *Acta oto-laryngol*, Vol. 66, pp. 357-368, Stockholm, 1968. /420
2. Caston, J., "Spontaneous Efferent Activity of the Ampular Nerves in the Frog," *J. Physiol.*, Vol. 62, p. 140, Paris, 1970a.
3. Caston, J., "Efferent Activity of the Ampullar Nerves Obtained by Stimulation of the Horizontal Semicircular Canals in the Frog," *J. Physiol.*, in press, Paris, 1970b.
4. Gleisner, L. and N. G. Henriksson, "Efferent and Afferent Activity Pattern in the Vestibular Nerve of the Frog," *Acta oto-laryngol.*, Supplement 192, pp. 90-103, Stockholm, 1963.
5. Ireland, P. E. and J. Farkashidy, "Studies on the Efferent Innervation of the Vestibular End Organs," *Ann. Otol.*, Vol. 70, pp. 490-503, 1961.
6. Ledoux, A., "The Semicircular Canals," *Acta med. belg.*, 236 pages, Bruxelles, 1958.
7. Rossi, G., "The Efferent Innervation of the Vestibular Receptors," *Acta oto-laryngol.*, Vol. 58, pp. 230-238, Stockholm, 1964.
8. Sala, O., "The Efferent Vestibular System: Electrophysiological Research," *Acta oto-laryngol.*, Supplement 197, 34 pages, Stockholm, 1965.
9. Schmidt, R. S., "Frog Labyrinthine Efferent Impulses," *Acta oto-laryngol.*, Vol. 56, pp. 51-64, Stockholm, 1963.
10. Wersaell, J., "Studies on the Structure and Innervation of the Sensory Epithelium of the Cristac Ampullares in the Guinea-pig," *Acta oto--laryngol.*, Supplement 126, pp. 1-85, Stockholm, 1956.

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